SILURIAN ODONTOPLEURID TRILOBITES FROM GOTLAND

by LARS RAMSKÖLD

ABSTRACT. Trilobites of the family Odontopleuridae are described from the Silurian of Gotland, Sweden. Twelve species and subspecies (nine named, of which four are new) are assigned to four genera. *Anacaenaspis gotlandensis* Bruton, 1967 is considered to be a junior subjective synonym of *Acidaspis pectinata* Angelin, 1854, which is therefore the type species of the genus. *Primaspis* (*Taemasaspis*) Chatterton, 1971 is regarded as a junior subjective synonym of *Dudleyaspis*, which in addition to the nominate subgenus includes *D.* (*Snoderaspis*) subgen. nov. *Ceratocephala barrandii* (Fletcher *in* Salter, 1853), *A. pectinata*, *Leonaspis corouata* (Salter, 1853) and *L. crenata* (Emmrich, 1844) are also known outside Gotland. New species and subspecies described are *D.* (*Dudleyaspis*) *hanrensis*, *D.* (*Dudleyaspis*) *uncifera*, *D.* (*Snoderaspis*) *krausi*, and *Leonaspis coronata bufo*.

THE first odontopleurid trilobite described from Gotland was *Odontopleura crenata* Emmrich, 1844, which is now referred to as *Leonaspis*. Angelin (1851, 1854) included a number of additional species in his monograph of Scandinavian trilobites. Lindström (1885) discussed these, but no new species were described by him or other workers until Bruton (1967) revised the Gotland odontopleurids, and gave a modern description of previously known and new species. Since Bruton's study, a wealth of new material has come to light, some from old collections, but most through recent collecting. This material includes previously unknown taxa and more complete specimens of most of the known species. It also provides information for a more satisfactory definition of the genera *Anacaenaspis*, *Dudleyaspis*, and *Primaspis*.

STRATIGRAPHY AND LOCALITIES

The stratigraphical distribution of the species as plotted in text-fig. 1 follows the same scheme as that in Ramsköld (1983). Again it must be emphasized that this distribution does not necessarily reflect the chronological appearance and disappearance of the various taxa. Locality names followed by numbers are defined in Laufeld (1974*b*), Larsson (1979), and Ramsköld (1983). Two new localities are described here in conformity with this system. DJUPVIKSVÄGEN 1, 635572 164170 (CJ 5512 2873), Eksta parish, *c.* 3950 m SSW of Fröjel church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 164 Hemse. Ditch exposure along north side of road, from the forest edge and 20 m south-east, *c.* 1100 m north-west of the intersection of road 140 with the road to Djupvik. Mulde Beds, undifferentiated. VALVE 2, 637352 164018 (CJ 7299 2859), Eskelhem parish, *c.* 2800 m NNW of Västergarn church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 160 Klintehamn. Exposure in ditch running south-east from road, then curving first north then south into the forest. The road/ditch intersection is *c.* 225 m south-east of the house at Valve. Slite Beds, Slite Marl.

For other localities twelve figure grid references are given according to the Swedish National Grid (Rikets nät) system whenever possible.

SYSTEMATIC PALAEONTOLOGY

The terminology employed here is essentially that of Harrington *et al.* (*in* Moore 1959). Lateral glabellar lobes and furrows are labelled following Jaanusson (1956, p. 37). Terms for the orientation used during photography are those of Whittington and Evitt (1954, p. 11). Specimens are deposited in

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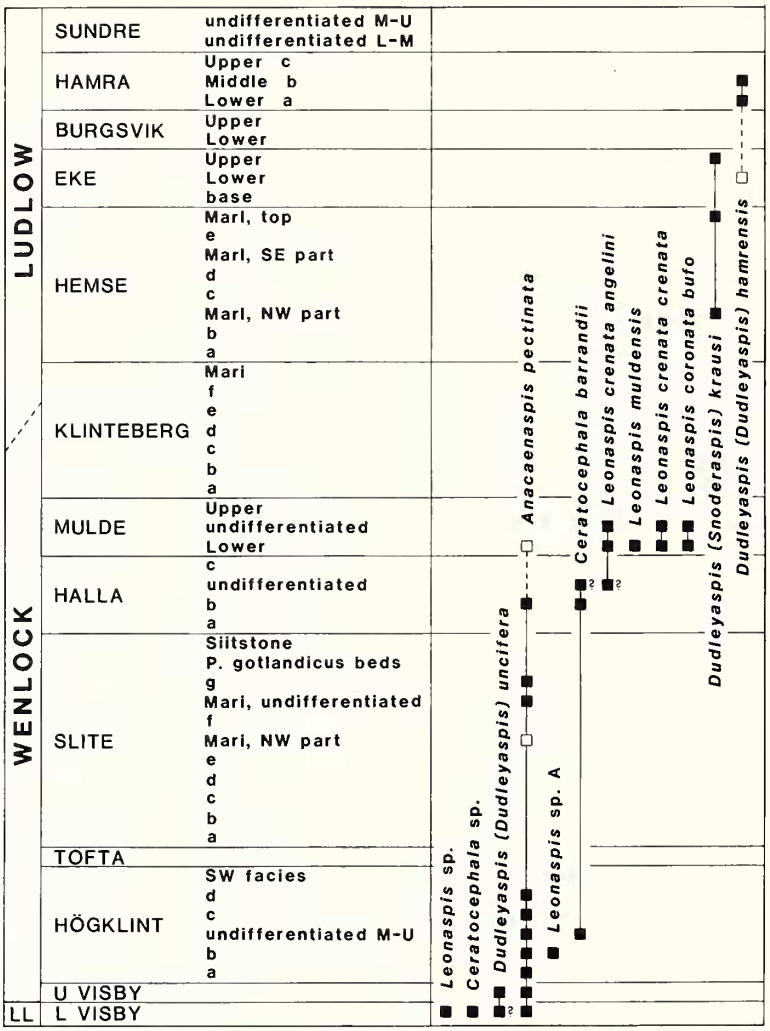
Naturhistoriska Riksmuséet, Stockholm (prefixed Ar), in the Type Collection of the Geological Survey of Sweden (SGU), and in the Royal Scottish Museum, Edinburgh (RSM). Unless stated otherwise, illustrations in the plates are of external surfaces of exoskeletons. All specimens were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. Most specimens with numbers beginning Ar51 were collected by the author; other collectors are indicated in the plate explanations when known.



TEXT-FIG. 1. Occurrence of Odontopleuridae in the different stratigraphical units of Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, and is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974*a*, p. 124).

Family ODONTOPLEURIDAE Burmeister, 1843
Subfamily ODONTOPLEURINAE Burmeister, 1843

Discussion. A re-evaluation of the genera *Anacaenaspis*, *Dudleyaspis*, and *Primaspis* is necessary on the basis of the Gotland material described here (for summary of previous concepts see Chatterton *et al.* 1979, p. 828, and Thomas 1981, pp. 83, 85). When Chatterton (1971) erected *Taemasaspis* as a subgenus of *Primaspis* he noted its close similarity and possible relationship to *Dudleyaspis* (as diagnosed by Bruton 1968). After transferring *Odontopleura portlockii* Hawle and Corda, 1847 (included by Bruton in *Dudleyaspis*) to *Taemasaspis*, Chatterton considered that the subgenus fitted best within *Primaspis*. However, several features indicate that *Taemasaspis* is closer to *Dudleyaspis* than to *Primaspis*, including the straight-eye ridge, the shape, size, and position of the genal spine, the wide thoracic axis, the insignificant fulcral swellings, and the disposition and relative sizes of the pygidial border spines. The widely separated eyes, set in a horizontal plane well below L1 and never overhanging the posterior border furrow due to their rather forward position, are also indicative of affinities with *Dudleyaspis*. Thomas (1981) noted these similarities and regarded *Taemasaspis* as a junior synonym of *Dudleyaspis*; this study confirms these similarities, and Thomas is followed here. A second subgenus of *Dudleyaspis*, *Snoderaspis*, is erected here. When Bruton (1967) erected *Anacaenaspis*, he selected as holotype of the type species *A. gotlandensis* a specimen that is recognized here as belonging to Angelin's (1854) species *pectinata*. The type species therefore becomes *A. pectinata*. This species belongs to a distinct and homogenous group of Silurian odontopleurines, which in addition includes *Acidaspis callipareos* Thomson, 1857, *Anacaenaspis gigantea* Šnajdr, 1978, *A. phasganis* Thomas, 1981, and *Primaspis kruegeri* Schrank, 1969. Generic status for this group seems justified, and *Anacaenaspis* is therefore recognized here. The genus is close to *Primaspis* Richter and Richter, 1917. *Primaspis* species fall into two morphological groups; the type species *P. primordialis* (Barrande, 1846), from the Bohemian Caradoc, and the remainder. Přibyl and Vaněk (1965) erected the subgenera *P.* (*Primaspis*) and *P.* (*Meadowtownella*), respectively, for the groups. These subgenera have rarely been used by subsequent workers. The *Meadowtownella* group is very coherent, and seems in many respects to be related, and perhaps ancestral to *Dudleyaspis*. *P. primordialis*, on the other hand, is similar in some features to *Anacaenaspis*, e.g. in the lengthened occipital ring and the overall shape of the pygidium. However, the free cheek of *primordialis* (figured Šnajdr 1956, pl. 2 (33), fig. 10) is not of *Anacaenaspis* type, but is similar to other *Primaspis* (i.e. the *Meadowtownella* group). Known *primordialis* specimens are not well preserved, but the available material seems to justify retaining *Primaspis* and *Anacaenaspis* as separate genera.

Genus ANACAENASPIS Bruton, 1967

Type species. Emended here; *Acidaspis pectinata* Angelin, 1854, from the uppermost Llandovery and Wenlock of Gotland (Lower Visby to Halla Beds), the Upper Llandovery of Scotland, and the Wenlock of Estonia.

Diagnosis. Occipital ring long (exsag.). Longitudinal furrow distinct. Antennal notch marked. Eye ridges curved, eye set close to posterior border furrow, level with L1. Genal spines very long, reaching behind thorax, base not raised markedly above lateral border. Ten to twelve long and stout cephalic border spines, the posteriormost the largest and at right angles to genal spine. Fulcral swellings large. Pygidium with major border spines much longer and stouter than, separated from, and set above the plane of, secondary border spines.

Remarks. Anacaenaspis is a clearly defined genus, although Bruton's (1967) concept of it was partly different from mine, because of the restricted amount of material available to him. Apart from the holotype of *A. gotlandensis*, all specimens assigned by Bruton to that species are referred here to *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov. The second species originally included, *A. emarginata* (Schmidt, 1885), is regarded here as a junior subjective synonym of *pectinata*.

The relationship of *Anacaenaspis* to *Primaspis* is discussed above. The genus is also close to *Acidaspis* Murchison, 1839, the major difference being the large median occipital spine in the latter.

Anacaenaspis pectinata (Angelin, 1854)

Plate 26, figs. 1–13; Plate 27, figs. 1–10; text-fig. 2

1851 Angelin, pl. 21, fig. 5 [illustration only, without name].
v* 1854 *Acidaspis pectinata* Angelin, p. 33 [referring to 1851 figure].
. *1885* *Acidaspis pectinata* Angelin; Lindström, p. 55.
. 1885 *Acidaspis emarginata* Schmidt, p. 23, pl. 1, fig. 1.
1889 *Acidaspis pectinata* Angelin ? = *Odontopleura ovata* Emmrich; Jaekel, p. 711 [*non* Emmrich, 1839].
1896 *Acidaspis pectinata* Angelin; Lake, p. 243.
1949 *Acanthaloma pectinata* (Angelin); Prantl and Přibyl, p. 139.
v. 1967 *Acidaspis pectinata* Angelin; Bruton, p. 234, pl. 35, figs. 3, 5, 6.
v. 1967 *Anacaenaspis gotlandensis* Bruton, p. 236, pl. 36, figs. 2–4, *non* pl. 35, fig. 10, pl. 36, fig. 5 [= *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov.].
. 1967 *Anacaenaspis emarginata* (Schmidt, 1885); Bruton, p. 237, pl. 35, fig. 14, pl. 36, fig. 1 [with synonymy list].
1969 *Primaspis gotlandensis* (Bruton); Schrank, p. 722 [*pars*].
1973 *Primaspis* (*Meadowtownella*) *gotlandensis* (Bruton); Přibyl and Vaněk, p. 303.
1978 *Anacaenaspis gotlandensis* Bruton; Šnajdr, p. 31 [*pars*].
v. *1979* *Acidaspis pectinata* Angelin; Bruton *in* Jaanusson *et al.*, p. 116.
v. *1979* *Anacaenaspis* sp.; Bruton *in* Jaanusson *et al.*, p. 116.
1979 *Anacaenaspis gotlandensis* Bruton; Chatterton *et al.*, p. 828 [*pars*].
1981 *Acidaspis pectinata* Angelin; Thomas, p. 81.
1981 *Anacaenaspis gotlandensis* Bruton; Thomas, p. 85 [*pars*].
. 1981 *Anacaenaspis dealgach* (Lamont, 1978); Clarkson and Howells, p. 529, pl. 81, fig. 2, pl. 82, figs. 1–4 [with synonymy list].
. 1982 *Anacaenaspis dealgach* (Lamont, 1978); Howells, p. 58, pl. 15, figs. 10, 15.

Lectotype. Selected here; Ar30867, incomplete cephalon, Plate 26, fig. 12*a–c*, used for the composite figure of Angelin 1851; refigured Bruton 1967, pl. 35, fig. 6; almost certainly from Högklint Beds, Visby area.

Bruton (1967, p. 234) thought that this specimen may be one of Angelin's (1851, 1854) syntypes. The shape of the genal spine, faithfully depicted by Angelin, is due to a postdepositional fracture and secondary rotation of the spine, a deformation unlikely to be exactly similar in any other specimen. In addition, the specimen (then largely embedded in matrix) was broken at some time into three pieces. None of the fractures reveals the presence of occipital spines, but it is obvious from the pieces that the cephalon must be broken across the occipital ring, as stated by Angelin, and lacking the left half. All these factors indicate that this is the specimen used by Angelin for his reconstruction of the cephalon. Additional preparation has now revealed the shape of the occipital ring,

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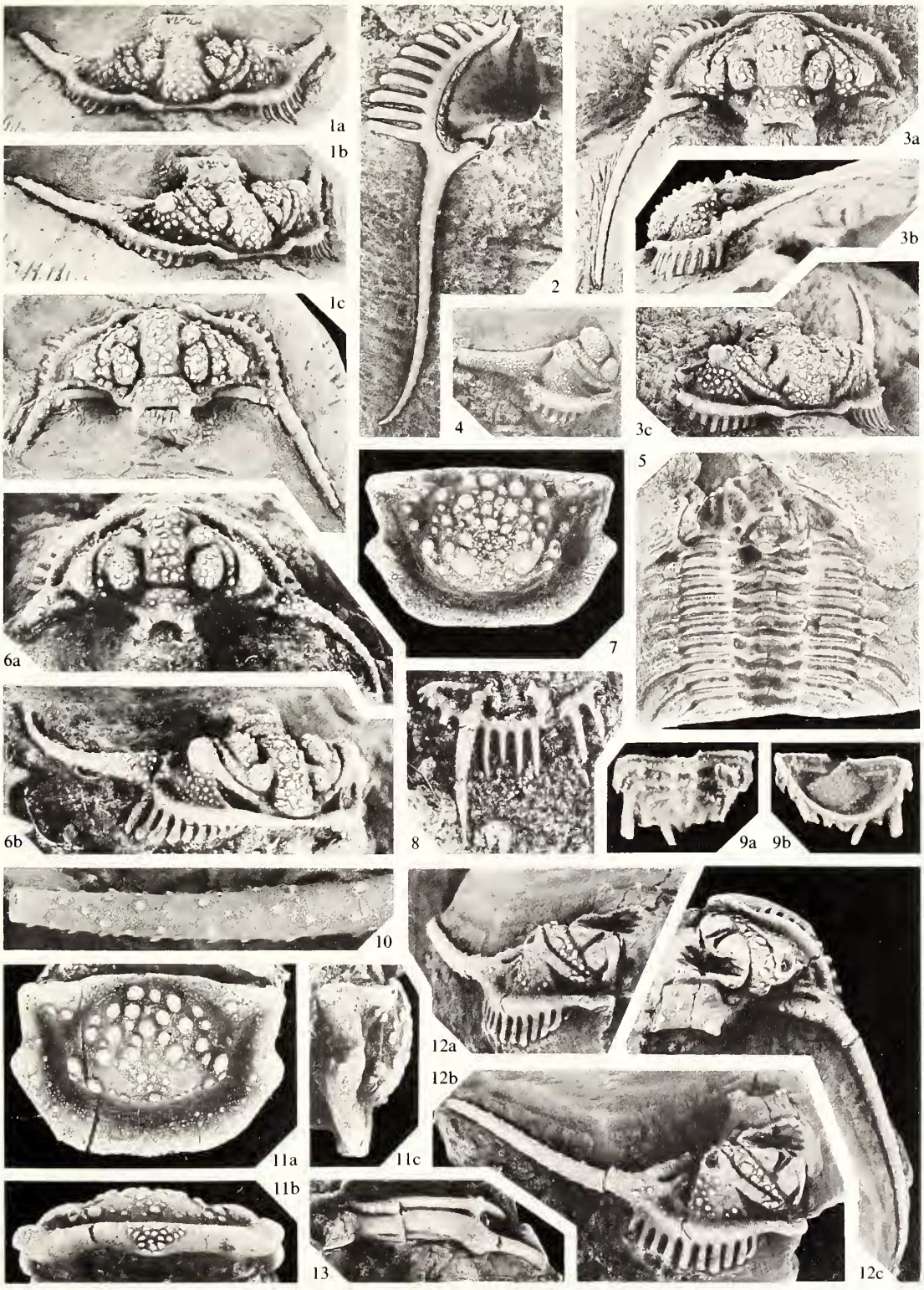
EXPLANATION OF PLATE 26

Figs. 1–13. *Anacaenaspis pectinata* (Angelin, 1854). Upper Visby Beds (9). Högklint Beds, unit a (2, 3), unit b? (12), unit d (5, 8). Slite Beds, Slite Marl (1, 4, 10, 11, 13). Halla Beds, unit b (6). Hörsne kanal (6), Ireviken 1 (2, 3), Rönnklint (9), Valbytte 1 (1, 10, 11, 13), Vattenfallsprofilen 1 (5, 8), Visby (12), shore of Eketräsk (4), Jaani Stage, Paramaja pank, Saarema, Estonia (7). 1*a–c*, Ar51358, cephalon, anterior, anterolateral, and exterior views, ×3. 2, Ar51629, partial cephalon with complete spine fringe and genal spine, interior view, ×2·5. 3*a–c*, Ar51630, cephalon, exterior, lateral, and anterolateral views, ×2·5. 4, SGU 1446, partial cephalon, anterolateral view, note dense tuberculation, ×4·5 (coll. G. Liljevall). 5, SGU 1448, flattened exoskeleton lacking pygidium, ventral view, note displaced hypostome, ×4 (coll. O. W. Wennersten 1890). 6, SGU 1447, small cephalon, exterior and anterolateral views, ×9 (coll. G. Liljevall 1910). 7, Ar51750, hypostome, exterior view, ×8 (coll. V. Jaanusson 1939). 8, Ar49890, small pygidium, ×10. 9*a, b*, Ar51709, slightly distorted transitory pygidium, dorsal and ventral views, ×18. 10, Ar51350, genal spine showing thorn-like tubercles with pore-openings, ×8. 11*a–c*, Ar51354, large hypostome, exterior, posterior, and lateral views, ×6. 12*a–c*, lectotype Ar30867, partial cephalon, figured Angelin 1851, pl. 21, fig. 5, refigured Bruton 1967, pl. 35, fig. 6, anterior, anterolateral, and exterior views, ×3. 13, Ar51351, partial thoracic segment, ×2.



RAMSKÖLD, *Anacaenaspis*

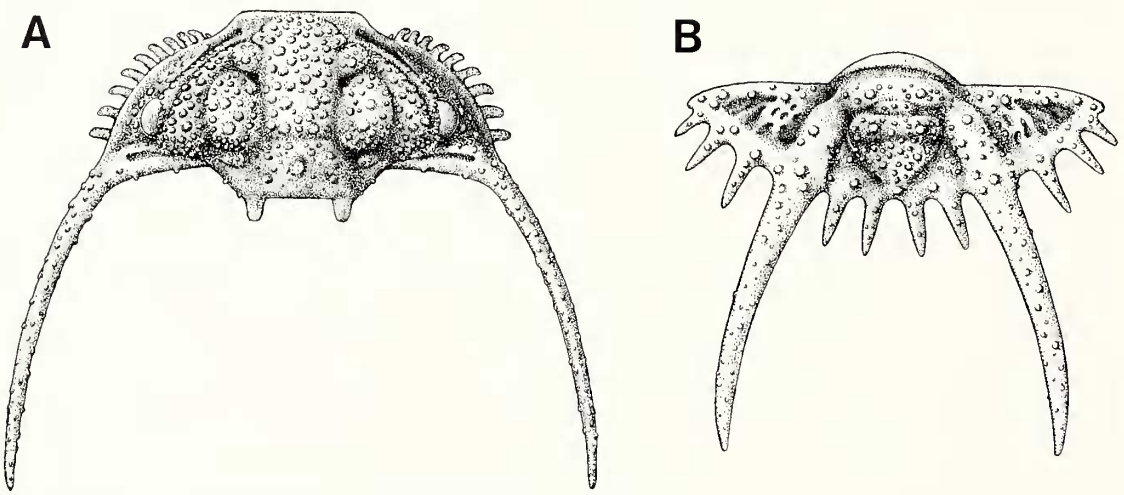
which (together with other features) necessitates a removal from *Acidaspis*. The pygidium figured by Angelin cannot be identified with certainty.

Additional material. The Scottish material from the Pentland Hills is of late Llandovery age (Clarkson and Howells 1981; see under 'Discussion' below). Estonian specimens are known from Koguva säär, Island of Muhu, and Paramaja pank, Saarema, both Jaani Stage (upper Wenlock; Bruton 1967). On Gotland this species ranges from the uppermost Llandovery to the upper Wenlock.

Localities. Lower and Upper Visby Beds: Lummelunda parish—Rönnklint (641181 165698). Upper Visby Beds: Västerhejde parish—Fridhem (638860 164375). Högklint Beds, unit a: Stenkyrka parish—Ireviken 1. Unit b: Visby parish—dump at Visby harbour (639275 164800), Västerhejde parish—Fridhem (638885 164425). Units b–d: Visby parish—Vattenfallsprofilen 1. Slite Beds, Slite Marl: Eskelhem parish—Valve 2, Fårö parish—Haganäs 1; the southern shore of Eketräsk, Othem parish—Slite, Sanda parish—Valbytte 1. Slite Beds, unit g: Othem parish—Slite. Halla Beds, unit b: Hörsne parish—Hörsne kanal (638493 166725). The holotype of *A. gotlandensis* Bruton, 1967, is stated to be from the Hemse Marl at Petesvik, Hablingbo parish (a now overgrown locality) but this is questionable since this species is not known otherwise from Ludlow strata. One fragment from Bolarve 1, Hejdeby parish, Slite Marl, north-western part, may also belong to this species. Some cheek fragments (Ar51536–51538) from the Mulde Beds, lower part, at Djupvik, Eksta parish, are similar in most respects to *A. pectinata*, but differ slightly in having several very large tubercles on the lateral border. A definite assignment cannot be made until more complete specimens are known.

Diagnosis. Two paired, short, blunt spines posterolaterally on occipital ring. Six or seven tubercle pairs on glabella. Ten or eleven stout, nearly cylindrical, cephalic border spines. Axial rings with two paired posterolateral and one median tubercle. Very coarse cephalic tuberculation, also on hypostome. Pygidium coarsely tuberculated except on pleural field.

Description. This species has been described recently by a number of authors (see synonymy), so that only new or important features are noted here. Occipital ring with sharply defined occipital lobes (Pl. 27, fig. 9), short median spine with occipital organ, posterior margin with two paired spines. Anterior branch of facial suture indicated by a discrete ridge running from eye towards antennal notch (Pl. 26, figs. 6*b*, 12*b*), posterior branch indicated by a strong ridge running from eye to genal angle. Genal spine very long, curved downwards distally. Border spines slightly spatulate, with serrated tips (Pl. 26, fig. 2). Lateral margin (but not posterior) slightly incurved at base of genal spine. Six pairs of conspicuous tubercles (and possibly an anterior small pair) present on median lobe of



TEXT-FIG. 2. *Anacaenaspis pectinata* (Angelin, 1854). A, reconstruction of cephalon, based mainly on Ar30867, Ar51358, and Ar51630, about ×3. B, reconstruction of pygidium, based on Ar51348, Ar51352, and Ar51573, about ×3.

glabella. Lateral border with three conspicuous tubercles decreasing in size forwards, situated above border spines 3–4, 5–6, and 7–8 (numbered from rear forwards). Genal spine with thorn-like tubercles with a pore-opening distally at their base (Pl. 26, fig. 10).

Rostral plate unknown. Hypostome (Pl. 26, figs. 7, 11*a–c*, Pl. 27, fig. 7*a–c*) with oval, gently inflated middle body. Very faint middle furrow possibly present laterally just in front of conspicuous lateral tubercle. Maculae indicated by two smooth, oval areas. Anterior border unbroken medially, though very short, defined by wide furrow. Lateral border with blunt, subtriangular anterior wing and prominent shoulder. On the inner edge of the doublure underlying the shoulder is a small posterior wing (Pl. 27, fig. 7*c*). Border behind shoulder wider (tr.), confluent with equally wide (sag.) posterior border. Posterior margin has flattened, densely tuberculated subtriangular area medially (Pl. 26, fig. 11*b*, Pl. 27, fig. 7*c*). Middle body with pair of prominent tubercles laterally. Small specimens with a few additional tubercles, large specimens have middle body densely tuberculated. Ventral surface (except maculae) densely granulated.

Thorax with ten segments. Anterior and posterior pleural spines very short on first segment, progressively larger posteriorly, anterior spine blade-like to bluntly cylindrical. Axis with paired tubercles. Posterior pleural ridge with prominent tubercle at fulcrum and one at mid length.

Axial furrow in pygidium very deep except anteriorly and overhung by second axial ring and terminal piece. Pleural areas depressed, with reticulate pattern of ridges and depressions (through differentiated skeletal thickness, mostly not visible ventrally). Posteriorly are two pairs of secondary spines, laterally are three similar pairs, the anteriormost smaller and merged with articulating process (Pl. 27, fig. 2). Secondary spines situated at slightly lower level than major spines; these curve slightly inwards and upwards distally. Paired tubercles on axial rings and terminal piece. Posterior border with major tubercle above each spine-base. Tubercles on main body of pygidium and proximal part of spines elongated, with slightly bulbous tips wider than at bases.

Ontogeny. The only known transitory pygidium (Pl. 26, fig. 9*a*, *b*) is 1·20 mm wide and slightly distorted. It is similar to a late transitory pygidium of *Primaspis ascitus* described by Whittington (1956*b*, pl. 2, fig. 9) in having large, paired axial tubercles, a feature lost later in *ascitus* but retained in adult stages of *pectinata*. The prominent tubercle on the posterior pleural ridge, a characteristic *pectinata* feature, is also present.

In the holaspid cephalon, L1 and L2 change during growth from a more equal size to L2 being much smaller, a change accompanied by a relative widening of the median glabellar lobe, and a reduction of eye size. The paired glabellar tubercles are retained also in large specimens, although less obvious than in small ones. The hypostome becomes relatively wider during growth, and the middle body becomes more tuberculated, while the tuberculate area on the posterior margin becomes smaller. The shape of the pygidium is fairly stable, the shortening of the secondary spines being the only marked change.

Discussion. The holotype of *Anacaenaspis gotlandensis* Bruton, 1967, has been examined, and no differences between it and *A. pectinata* have been found. The occipital ring of the specimen is heavily worn, with no spines preserved, but the shape of what remains does not preclude their original presence. In addition, on the anterior axial rings of the thorax there are remains of one anteromedian and two posterolateral tubercles. Since these rings commonly have tubercles repeating the spine pattern of the occipital ring, corresponding occipital spines are to be expected (the tubercles on the axis are also preserved on a specimen from the Pentland Hills, Scotland, Pl. 27, fig. 10, and on unfigured Gotland material). The holotype has only the bases of the border spines preserved, and they cannot therefore be seen in dorsal view, a fact considered diagnostic by Bruton (but see Pl. 26, fig. 2 for length of complete spines). Other features typical of *A. pectinata* are all present, such as the strong posterior sutural ridge, the shape of the cheek border, carrying the same number of spines, and the tubercle pattern on the cheek and pleurae.

Bruton (1967) described and figured the holotype of *Acidaspis emarginata* Schmidt, 1885, from the upper Wenlock of Estonia, and listed the features distinguishing it from *A. gotlandensis* (= *A. pectinata*). The only known *emarginata* cephalon is similar to *pectinata* in all observable features, and the Estonian hypostome (Pl. 26, fig. 7) is identical to the large Gotland hypostome (Pl. 26, fig. 11*a–c*). *A. emarginata* is regarded here as a junior subjective synonym of *A. pectinata*. *A. dealgach* (Lamont, 1978; see Clarkson and Howells 1981, and Pl. 27, fig. 10 here), from the Upper Llandovery of Scotland, is identical to the Gotland material and is also considered to be a junior subjective synonym of *pectinata*. *A. callipareos* (Thomson, 1857; see Howells 1982), from the Lower Llandovery of Girvan, Scotland, is distinguished from *pectinata* mainly in lacking occipital spines and paired tubercles on the glabella, in the indented posterior margin, weak furrows and smooth surface of the

hypostome, in the granulate rather than tuberculate cephalon, and in the functional facial sutures. As so far known, these differences also apply to the Bohemian Llandovery *A. gigantea* Šnajdr, 1978, which is also distinguished by having seventeen to nineteen marginal spines in the pygidium. *A. kruegeri* (Schrank, 1969), from a late Wenlock erratic from Neu Nieköhr, DDR, differs from *pectinata* mainly in lacking occipital spines and in having eighteen rather than twelve pygidial border spines. The differences listed by Schrank (1969, p. 722) refer largely to the specimens included here in *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov. The British Wenlock *A. phasganis* Thomas, 1981, is closer to *pectinata* than recorded by Thomas (1981, p. 85), differing mainly in lacking occipital spines and in having a more adaxially placed eye.

As with the transitory pygidium (see above), the hypostomes assigned here to *A. pectinata* bear some resemblance to that of the American Middle Ordovician *Primaspis ascitus* Whittington, 1956*b* (pl. 1, figs. 18–21; note the tuberculate, flat area on the posterior margin) and indicates the close relationship between these genera. It also shows similarities to the hypostome of *A. cincinattiensis* Meek, 1873, also from the Middle Ordovician of North America (see Whittington 1956*a*, pl. 59, figs. 3, 6).

Genus DUDLEYASPIS Prantl and Přibyl, 1949

Discussion. Two subgenera are recognized here (see discussion under Odontopleurinae and respective subgenus). They both have the occipital ring at least five times as broad as long; occipital lobes present; eye lobe set at a level below L1, not in contact with posterior border furrow, transverse width between palpebral lobes at least one and one-third the length of glabella; anterior and posterior branches of (nonfunctional) facial suture run on sutural ridges; genal spine slim, not exceeding length of glabella; posterior border incurved at base of genal spine; thorax with ten segments, axis wide, fulcral swelling small; pygidium with two pairs of spines between major spines, all spines evenly spaced, at about the same level. *A. harborti* Richter and Richter, 1926, may belong to *Dudleyaspis*, but is not known well enough to be definitely assigned.

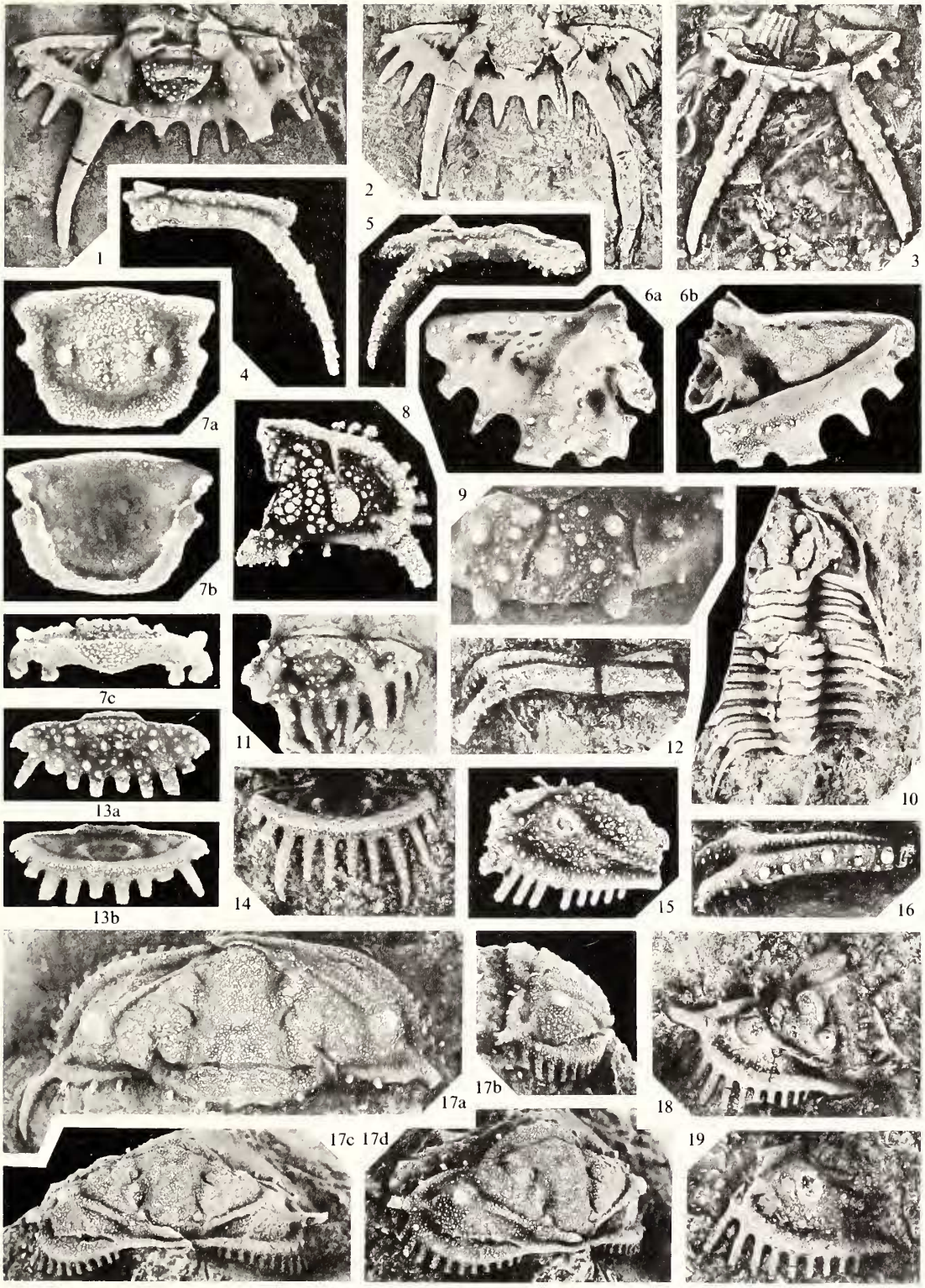
EXPLANATION OF PLATE 27

Figs. 1–10. *Anacaenaspis pectinata* (Angelin, 1854). Upper Visby Beds (4, 7–9), Högklint Beds, unit b (1, 3), Slite Beds, Slite Marl (2, 6), Halla Beds, unit b (5). Fridhem (3), Hörsne kanal (5), Rönnklint (4, 7–9), Valbytte 1 (6), Valve 2 (2), dump at Visby harbour (1), Wether Law Linn Formation (Upper Llandovery), Pentland Hills, Scotland (10). 1, Ar51348, pygidium, major spine deformed distally, × 3. 2, Ar51573, pygidium, × 3. 3, SGU 1449, pygidium, ventral view, × 4 (coll. J. G. Andersson). 4, Ar51647, partial thoracic segment, × 6. 5, SGU 1450, partial thoracic segment, × 10 (coll. G. Holm). 6*a*, *b*, Ar51352, partial large pygidium, dorsal and ventral views, × 3. 7*a–c*, Ar51645, small hypostome, exterior, interior, and posterior views, × 12. 8, Ar51644, partial small cephalon, exterior view, × 12. 9, Ar51643, occipital ring with complete spines and median organ, × 12. 10, RSM GY 1983.18.1, latex cast of external mould of exoskeleton lacking pygidium, × 4.

Figs. 11–18. *Dudleyaspis* (*Dudleyaspis*) *hamrensis* sp. nov. Hamra Beds, unit a (11–17), unit b (18). Gisle 2 (11, 12, 14, 16), Kättelviken 1 (13, 15, 17), Majstre 1 (18). 11, Ar51550,* pygidium, × 6. 12, Ar51545,* partial thoracic segment, × 4. 13*a*, *b*, Ar51618,* pygidium, dorsal and ventral views, × 6. 14, Ar51549,* small pygidium, ventral view, × 9. 15, Ar51616,* partial cephalon, anterolateral view, × 5. 16, Ar51544,* partial thoracic segment, × 4. 17*a–d*, holotype Ar51568, cephalon, exterior, lateral, anterior, and antero-lateral views, *a* × 4, *b–d* × 3. 18, Ar51637,* partial cephalon, anterolateral view, × 6.

Fig. 19. *Dudleyaspis* (*Dudleyaspis*) *hamrensis* sp. nov.? Ar51638, partial cephalon, anterolateral view, Gannor 1, Eke Beds, lower part, × 6.

* Paratypes.



RAMSKÖLD, *Anacaenaspis*, *Dudleyaspis*

Subgenus DUDLEYASPIS (DUDLEYASPIS) Prantl and Přibyl, 1949

Subjective synonym: *Primaspis* (*Taemasaspis*) Chatterton, 1971

Type species. *Acidaspis quinquespinosa* Lake, 1896, from the Much Wenlock Limestone Formation, Dudley, West Midlands, and Sedgley, Staffordshire, Great Britain.

Diagnosis. Cephalon wide and short; width to length 2·3 : 1–3·2 : 1. Eye set closer to axial furrow than to lateral border furrow. Facial suture with posterior branches diverging backwards at 120–180°. Genal spine directed obliquely outwards.

Dudleyaspis (*Dudleyaspis*) *hamrensis* sp. nov.

Plate 27, figs. 11–18

Name. From the type stratigraphical unit.

Holotype. Ar51568, cephalon, Pl. 27, figs. 17*a–d*, from Kättelviken 1, Vamlingbo parish, Hamra Beds, unit a.

Paratypes. From the type locality, Ar51588, Ar51615–51619. From Gisle 2, Öja parish (Hamra Beds, unit a), Ar51541–51550. From Hamra Beds, unit b, Sundre parish: Majstre 1, Ar51637; north of Hoburgen, Ar51551. In total seven partial cephala, seven thoracic segments, and six pygidia. A partial cephalon, Ar51638, from the lower Eke Beds at Gannor 1, Lau parish, may also belong to this species.

Diagnosis. Posterior cephalic margin with five very small spine pairs plus equally small median spine. Eyes set wide apart opposite anterior half of L1. Pygidium with six pairs of spines.

Description. Cephalon subtrapezoidal, highly vaulted in anterior view (Pl. 27, fig. 17*c*). Occipital ring occupying half of cephalic width (excluding spines). Occipital lobes very weakly defined. L3 elongate, directed at about 45° to sagittal line, with slightly bulbous tip. Longitudinal furrow wide, shallow. Axial furrow very weak. Eye ridge merging anteriorly with lateral extension of frontal lobe. Eye set exactly mid-way between axial and lateral border furrow. Cheek area between eye ridge/palpebral lobe and axial furrow large. Anterior branch of facial suture indicated by indistinct ridge, posterior branch not visible close to eye; a fairly strong sutural ridge appears near genal angle. Lateral border with eleven almost vertical spines (a twelfth knob-like anteriormost spine may be present), cylindrical, straight, blunt, the posteriormost slightly less than normal to genal spine. Three stout, elongated tubercles present on border, above border spines 1–2, 3–4, and 5–6 (counted from rear forwards), increasing in size backwards. Entire cephalon except deepest parts of furrows with a fine, spiny tuberculation. Six or seven pairs of slightly larger tubercles are barely discernible on median lobe of glabella.

Rostral plate and hypostome unknown. Thoracic segments (Pl. 27, figs. 12, 16) with axis over one-third of width between fulcra. Anterior pleural ridge widening (exsag.) distal to fulcrum into large, blade-like anterior spine. Posterior ridge produced into proximally downward-flexed, laterally more horizontal spine. On a presumed anterior segment the spine is transverse or curved slightly anteriorly, on probable posterior segments it curves backwards through 90°. Axial ring and posterior pleural ridge with three to four large, elongated tubercles each.

Pygidium (Pl. 27, figs. 11, 13, 14) with second axial ring bounded by wide (sag.) anterior and distinct posterior furrows. Terminal piece merging with border posteriorly. Pleural areas strongly depressed. Posterior to articulating process and a diminutive spine are two secondary border spines, followed by major spine and two further secondary spines. Axial rings and terminal piece each with a pair of spinose tubercles; conspicuous tubercles also at bases of all border spines.

Discussion. This species has a pygidium almost identical to that of *D.* (*D.*) *quinquespinosa*, but differs in its more vaulted cephalon, the number and size of spines on the posterior cephalic margin, the more anterolaterally situated eyes, and the only partly developed sutural ridges. It is more similar to the American upper Wenlock or lower Ludlow *D.* (*D.*) *desolator* Campbell, 1967, but is distinguished by the number and size of the posterior cephalic spines, and the slightly more abaxially set eyes. The American *D.* (*D.*) *vanhornei* (Weller, 1907), from the Niagaran dolomites, is clearly related to the above species, but is not sufficiently well known to permit a detailed comparison. These four species form a fairly tight group within *D.* (*Dudleyaspis*). The remaining species referred here to the

subgenus; *Primaspis* (*Taemasaspis*) *campbelli* Chatterton, 1971 (Australian Emsian or Eifelian), *Odontopleura bowningensis* Etheridge and Mitchell, 1896 (Australian Ludlow), *Odontopleura Portlockii* Hawle and Corda, 1847 (Bohemian and British Wenlock), and *D.* (*D.*) *uncifera* sp. nov. (see below), all differ from *D.* (*D.*) *liamrensis* (and its allies) by having a non-spinose occipital ring, genal spine projecting sublaterally, base level with lateral border anterior to strong anteriorward flexure of posterior margin, weak sutural ridges, and major spines on pygidium considerably larger than secondary spines. *Taemasaspis llandoveryana* Šnajdr, 1975 (see Šnajdr 1978 for complete description), from the Bohemian Llandovery, does not show close similarities to the above species, and cannot be included in *Dudleyaspis*, but seems to be morphologically (and stratigraphically) intermediate between *Primaspis* and *Odontopleura*.

Dudleyaspis (*Dudleyaspis*) *uncifera* sp. nov.

Plate 28, figs. 1–11; Plate 30, fig. 17

v. *1979 Dudleyaspis*? sp. indet; Bruton *in* Jaanusson *et al.*, p. 116.

Name. The name *uncifera* (Latin for 'hook-bearing') was used on a label written by G. Lindström, but it has never been published.

Holotype. Ar51652, cephalon with four articulated thoracic segments, Plate 28, fig. 1*a–d*, from the small point south of Kopparsvik, Visby, Upper Visby Beds.

Paratypes. ?Lower Visby Beds: Stenkyrka parish—south-west of Balsklint, 0–2 m a.s.l. (SGU 1453), Visby parish—Norderstrand (Ar5074). Upper Visby Beds: Lummelunda parish—Rönnklint (641181 165698) (Ar51640a–k; parts of cephalon, thorax and pygidium from one individual, Ar51641–51642). Västerhejde parish—Högklint (SGU 1451). Visby parish—Vattenfallsprofilen 1, 1·7–1·9 m a.s.l. (SGU 1452). Several fragments from the Lower Visby Beds at Rönnkling may also belong to this species.

Diagnosis. Cephalon very wide and short; width to length 3·2 : 1·0. Axial furrow almost effaced along glabella. Lateral glabellar furrows shallow, with an additional furrow on L1. L2 and L3 ridge-shaped. Posteriormost border spine straight and blunt, subparallel to short genal spine. Cephalon with fine granulation of low relief. Posterior pleural spines on thorax very stout, short, barbed. Pygidium with shallow axial and inter-ring furrows, seven pairs of spines, major spine stout, blunt.

Description. Cephalon subtrapezoidal. Occipital ring with occipital organ (Pl. 28, fig. 1*d*). Occipital lobes large. L1 twice as long (exsag.) as wide, divided into two parts by shallow furrow starting at inner end of S1 and curving laterally and posteriorly to join axial furrow. L2 small, elongated, defined faintly laterally. L3 similar in shape to L2 but smaller and almost transverse. Longitudinal furrow barely visible. Eye ridges straight, diverging at about 110°. Eyes set wide apart opposite posterior half of L1. Facial suture fused, anterior branch indicated by a faint ridge, posterior branch indicated by a short, weak ridge near genal angle. Field of cheek with reticulate pattern (of genal caecae?). Ventrally on lateral border are ten (and possibly a small eleventh) pointed, strongly curved spines, except the posteriormost which is cylindrical with an abrupt, blunt end. Genal spine small, proximally directed transversely (in dorsal view) and downwards. Median lobe of glabella carries seven obvious pairs of tubercles (Pl. 28, figs. 1*b*, 11), major tubercles on fixed cheek and eye ridge arranged symmetrically. Field of cheek smooth or with very sparse, fine granulation, cephalon otherwise very finely and densely granulated. Rostral plate and hypostome not known.

Thoracic segments with pleural ridges of low relief. Anterior pleural spine straight to curved backwards, cylindrical to slightly flattened, pointed, with barbed anterior and posterior edges. Posterior spine stout, barbed, almost transverse on anterior segments, posterior to this curved backwards, flexed strongly down at fulcrum. Pleurae with a few very small tubercles, spines densely and coarsely granulated.

Pygidium with ankylosed articulating half ring in anterior inter-ring furrow, second ring indistinctly separated from subtriangular terminal piece. Seven pairs of border spines, the fourth the major, anteriormost spine very small (Pl. 28, figs. 2, 8). Major spine thickest at about mid length, gently curved upwards and inwards distally. Secondary spines pointed, less than half the length of major spines. Tuberculation fairly sparse, no obvious paired tubercles on axis. Secondary spines with two rows of small tubercles. Spines densely granulated, surface between tubercles otherwise almost smooth.

Discussion. This species is easily distinguished from all other *Dudleyaspis* by the almost effaced axial and lateral glabellar furrows, and the shape of the posterior pleural spines in the thorax. A unique feature is the furrow dividing L1. The closest species appears to be *D.* (*D.*) *hamrensis* sp. nov. (cf. Pl. 27, fig. 17*a* with Pl. 28, fig. 1*c*), although that species belongs to the closely knit group around the type species (see p. 248).

Subgenus DUDLEYASPIS (SNODERASPIS) subgen. nov.

Name. From the type locality of the type species, and Greek *aspis*, shield.

Type species. Dudleyaspis (*Snoderaspis*) *krausi* sp. nov., from the Hemse and Eke Beds (lower-middle Ludlow), Gotland.

Diagnosis. Cephalon very close to semicircular, width to length 2 : 1. Eye set very anterolaterally, opposite anterior half of L1, three-quarters way from axial to lateral border furrow. Eye ridges diverging at 110–120°. Facial suture with posterior branches diverging at close to 90°. Genal spine curved backwards in horizontal plane. Anterior pleural spine on thoracic segments needle-like, posterior spine long, slender, barbed.

Discussion. This subgenus is similar to previously known *Dudleyaspis* in having a straight eye ridge and a lateral eye position, in the incurvation of the posterior border at the base of the fairly small genal spine, the shape, size, and number of both cephalic and pygidial border spines, and the fine surface tuberculation. However, the course of the (non-functional) facial suture and the extreme eye position in the semicircular cephalon are features sufficiently different to warrant a new, as yet monotypic, subgenus.

Dudleyaspis (*Snoderaspis*) *krausi* sp. nov.

Plate 29, figs. 1, 2, 4, 8–10, 12, text-fig. 3

. 1895 *Acidaspis* n. sp. Lindström, p. 11.
v. 1967 *Anacaenaspis gotlandensis* Bruton, p. 236 [*pars*], pl. 35, fig. 10, pl. 36, fig. 5, *non* figs. 1–4 [= *Anacaenaspis pectinata* (Angelin, 1854)].
v. 1967 *Anacaenaspis* aff. *gotlandensis* Bruton, p. 237 [*pars*], pl. 35, figs. 7–9.
1969 *Primaspis gotlandensis* (Bruton, 1967); Schrank, p. 722 [*pars*].
1978 *Anacaenaspis gotlandensis* Bruton; Šnajdr, p. 31 [*pars*].
1981 *Anacaenaspis gotlandensis* Bruton, 1967; Thomas, p. 85 [*pars*].
1982 *Anacaenaspis gotlandensis* Bruton, 1967; Howells, p. 58 [*pars*].

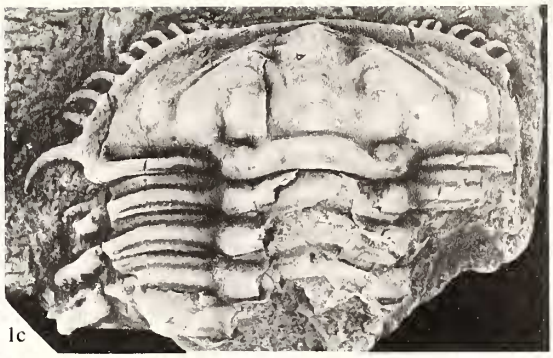
EXPLANATION OF PLATE 28

Figs. 1–11. *Dudleyaspis* (*Dudleyaspis*) *uncifera* sp. nov. ?Lower Visby Beds (8), Upper Visby Beds (1–7, 9–11). Point south of Kopparsvik, Visby (1), Högklint (4), Rönnklint (2, 3, 5, 7, 9–11), Vattenfallsprofilen 1 (6), coast south west of Balsklint (8). 1*a–d*, holotype Ar51652, cephalon with four thoracic segments, anterolateral, anterior, and exterior views, and enlargement showing granulation and median occipital organ, *a–c* ×2, *d* ×13 (coll. G. Lindström 1897). 2*a–c*, Ar51640k,* pygidium, dorsal, posterior, and ventral views, ×5. 3, Ar51641,* partial small pygidium, ×9 (coll. V. Jaanusson 1981). 4, SGU 1451,* eight (seven articulated) thoracic segments and pygidium, ×2·5 (coll. H. Hedström 1921). 5, Ar51640c,* cheek fragment with genal spine and part of spine fringe, all spines complete, interior view, ×5. 6, SGU 1452,* partial distorted cephalon, anterolateral view, ×3 (coll. G. Liljevall 1908). 7, Ar51640b,* partial cephalon, exterior view, ×4. 8, SGU 1453,* small pygidium, ventral view, ×9 (coll. G. Liljevall 1911). 9, Ar51640f–h,* partial thoracic segments, anterior pleural spine intact on middle specimen, ×5. 10*a*, *b*, Ar51640e,* three (one displaced) thoracic segments, anterolateral and dorsal views, ×5. 11, Ar51640a,* cephalic fragment showing paired tubercles on glabella, ×5.

* Paratypes.

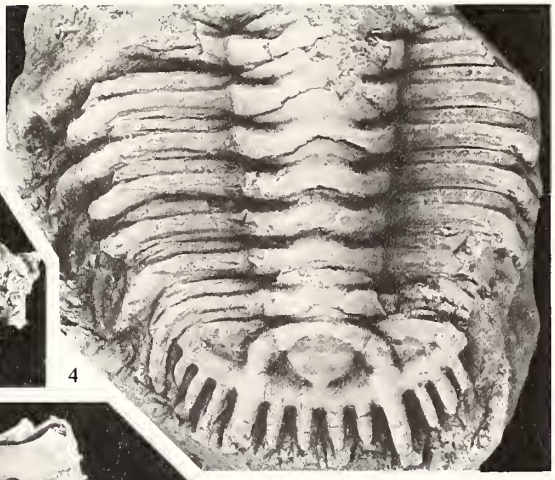

1a


1b


1c


2a


3


4


2b


5


2c


8

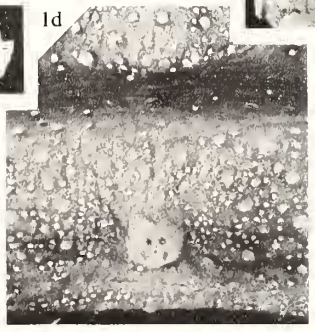

6


7


9


10a


10b


1d


11

RAMSKÖLD, *Dudleyaspis*

Name. After Mr Werner Kraus, who collected the holotype.

Holotype. Ar51757, cephalon, Plate 29, fig. 4*a–d*, from Snoder 2, Silte parish, Hemse Marl, north-western part, Hemse Beds (lower Ludlow).

Paratypes. From the Hemse Marl, north-western part: Silte parish—Snoder 1 (Ar51566), Snoder 2 (Ar51349, Ar51611). Hablingo parish—Hemmungs 1 (Ar51796), Petesvik (Ar30871, figured Bruton 1967, pl. 36, fig. 5, correct magnification × 4). Hemse Marl, top: Lau parish—Lau kanal (= Gannor; Ar30806*a–b*, figured Bruton 1967, pl. 35, fig. 10). Unknown locality, probably Hemse Beds (Ar30811, Ar30817—figured Bruton 1967, pl. 35, figs. 7–9, correct magnification figs. 7, 8 × 2). Eke Beds, upper part: Lau parish—Lau Backar 1 (Ar51598, Ar51599, Ar51611–51614). In total four complete and seven partial cephala, one hypostome, some thoracic segments, and three pygidia.

Diagnosis. As for subgenus.

Description. Occipital ring with faint occipital lobes, posterior margin slightly concave medially. Median occipital organ present (Pl. 29, fig. 4*d*). Median lobe of glabella parallel-sided, rather convex (tr., sag.). Longitudinal furrow deep. L3 small, distinct. Eye ridge running from just in front of L3 to small palpebral lobe. Area bounded by eye ridge/palpebral lobe and axial furrow very large, S-shaped in transverse profile, convex (exsag.). Eye situated at a level much below L1 (Pl. 29, fig. 4*c*). No palpebral furrow. Anterior branch of facial suture indicated by indistinct ridge on cheek, then curves across lateral border to antennal notch, posterior branch indicated by narrow ridge running straight from eye towards genal angle. Genal spine as long as glabella. Lateral border bearing row of twelve to thirteen gently curved, pointed spines ventrally (the number can vary even in the same individual, see Pl. 29, fig. 4*c*), the posteriormost at an angle of about 60° to border and genal spine. Posterior margin strongly incurved at base of genal spine. Antennal notch distinct. Entire cephalon except doublure with dense, fine, and even tuberculation.

Rostral plate unknown. The available hypostome (Pl. 29, fig. 1*c*) is distorted, slightly wider than long. Middle body as long as wide, inflated, extremely weak middle furrow possibly present at about mid length, maculae indicated by lack of tuberculation and darker colour. Anterior wing fairly large, lateral border narrow (tr.), with weak shoulder. Lateral border furrow narrow, distinct. Posterior border not preserved. Entire hypostome except anterior wing and maculae with dense, spiny tuberculation.

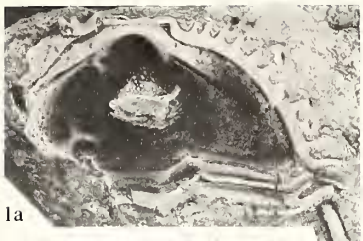
Thoracic segments with pleural ridges inflated, fulcral swellings faint. Posterior spine close to transverse proximally, curving gently backwards distally. Anterior spine straight, subparallel to posterior spine. Spines on first segment shortened (Pl. 29, fig. 1*b*), reaching full size on third segment. Pleural ridges with approximately two rows of spinose tubercles, tuberculation also on axis, posterior flange, spines, and in pleural furrow.

EXPLANATION OF PLATE 29

Figs. 1, 2, 4, 8–10, 12. *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov. Hemse Marl, north-western part, Hemse Beds (1, 4, 8, 9, 12), Eke Beds, upper part (2, 10). Petesvik (8), Snoder 1 (1), Snoder 2 (4, 9, 12), Lau Backar 1 (2, 10). 1*a–c*, Ar51566,* partial cephalon with displaced hypostome and two articulated thoracic segments, ventral view, enlargement of pleural spines (tips lost), and oblique view of hypostome lacking posterior border, *a* × 2, *b* × 5, *c* × 5·5. 2, Ar51611,* partial cephalon, exterior view, × 3. 4*a–d*, holotype Ar51757, cephalon, dorsal, anterolateral, and anterior views, and enlargement of median occipital organ, *a–c* × 2, *d* × 10 (coll. W. Kraus 1981). 8, Ar30871,* pygidium, figured Bruton 1967, pl. 36, fig. 5, × 4 (coll. G. Lindström). 9, partial cephalon belonging to Mr W. Kraus, Niedernhausen, dorsolateral view, × 2. 10*a*, *b*, Ar51614,* partial pygidium, ventral and dorsal views, × 4. 12*a*, *b*, Ar51349,* partial thoracic segment, dorsal and dorsolateral views, × 5.

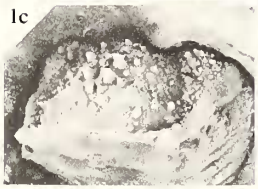
Figs. 3, 5–7, 11. *Leonaspis crenata* (Emmrich, 1844) *angelini* (Prantl and Přibyl, 1949). ?Halla Beds (6), Mulde Beds, lower part (11), undifferentiated (3, 5, 7). Blåhäll 1 (11), Djupviksvägen 1 (3), Lilla Karlsö (6), Nordervik (5, 7). 3*a*, *b*, Ar51368b, cranidium, anterior and exterior views, × 6·5. 5*a*, *b*, Ar51653, cranidium, exterior and anterior views, × 5. 6*a–c*, holotype Ar30859, complete specimen, figured Angelin 1854, pl. 22, fig. 14, refigured Bruton 1967, pl. 34, figs. 4–6, enlargement of pygidium, enlargement of pleurae, and posterior view, *a*, *b* × 6, *c* × 3. 7, Ar51654, partly disarticulated thorax and pygidium, oblique dorsolateral view, × 3. 11, Ar51369b, partial thoracic segment, note granulation on anterior pleural ridge, × 7.

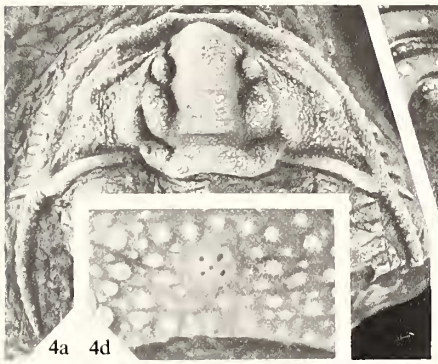
* Paratypes.


1a

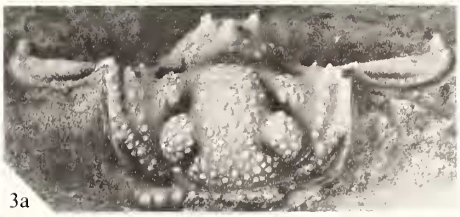

1b

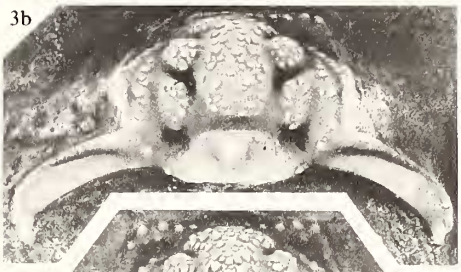

2

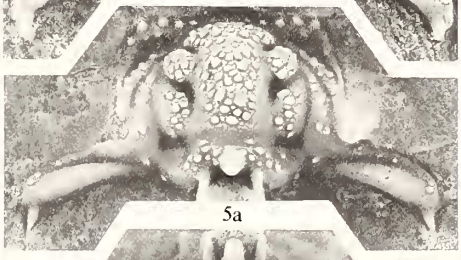

1c


4a 4d


6a


3a


3b


5a


5b


4b

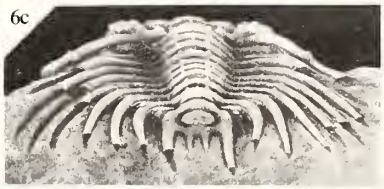

4c


8


6b


7


9


6c


10a

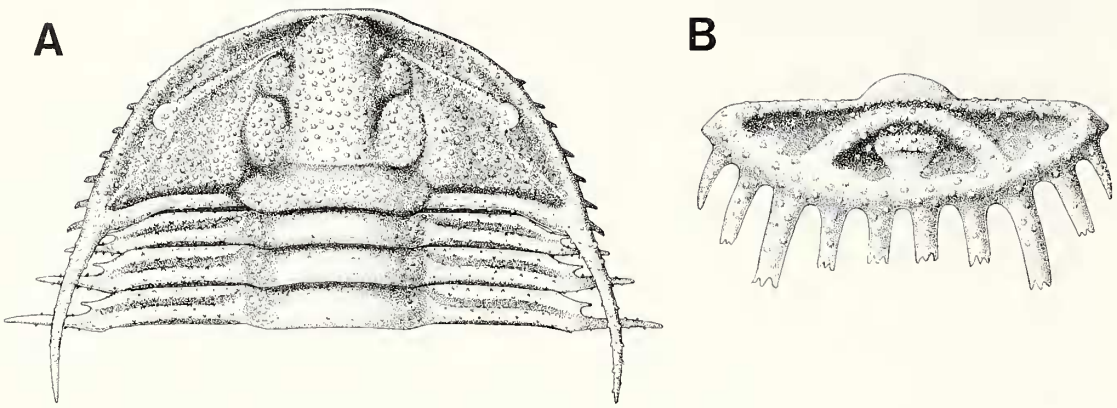

10b


11


12a


12b

RAMSKÖLD, *Dudleyaspis*, *Leonaspis*



TEXT-FIG. 3. *Dudleyaspis* (*Snoderaspis*) *krausi* subgen. and sp. nov. A, reconstruction of cephalon and part of thorax, based on Ar30817, Ar51566, and Ar51757, × 3. B, reconstruction of pygidium, based on Ar30817 and Ar30871, × 3.

Pygidium (Pl. 29, figs. 8, 10) with anterior axial ring continuous with pleural ridges and together with these forming a semicircle. Second ring half as wide (tr.), indistinctly separated from subtriangular terminal piece. Axial furrow very deep alongside terminal piece and second ring, indistinct anteriorly. Pleural areas strongly depressed. Two slender secondary spines on each side of only slightly stouter major border spines, which are of unknown length. Doublure (Pl. 29, fig. 10*a*) raised medially into spinose, transverse ridge. Entire pygidium with rather fine, sparse tuberculation, densest on axis, anterior border, and spines. No paired tubercles on axis or major tubercles at bases of spines.

Genus LEONASPIS Richter and Richter, 1917

Type species. Odontopleura Leonhardi Barrande, 1846; from the Kopanina Formation (Ludlow), Kolednik, Beroun, Czechoslovakia.

Discussion. The diagnosis of Whittington (1956*b*, p. 206) is followed here. Bruton (1967) described and discussed four *Leonaspis* species from Gotland, all from the Mulde Beds or from probable corresponding beds on the Karlsö islands. These species present difficulties in interpretation because all four type specimens either lack important structures, or come from localities that are either known imprecisely or are inaccessible for re-collecting. Most of the described material consists of water-worn specimens, although often complete individuals, from the harbour at Djupvik, Eksta parish, where collecting is no longer possible. New material from slightly higher horizons in the Mulde Beds have supplied additional information on these species, and they are in part reinterpreted here.

Leonaspis crenata crenata (Emmrich, 1844)

Plate 30, figs. 5, 7; text-fig. 4

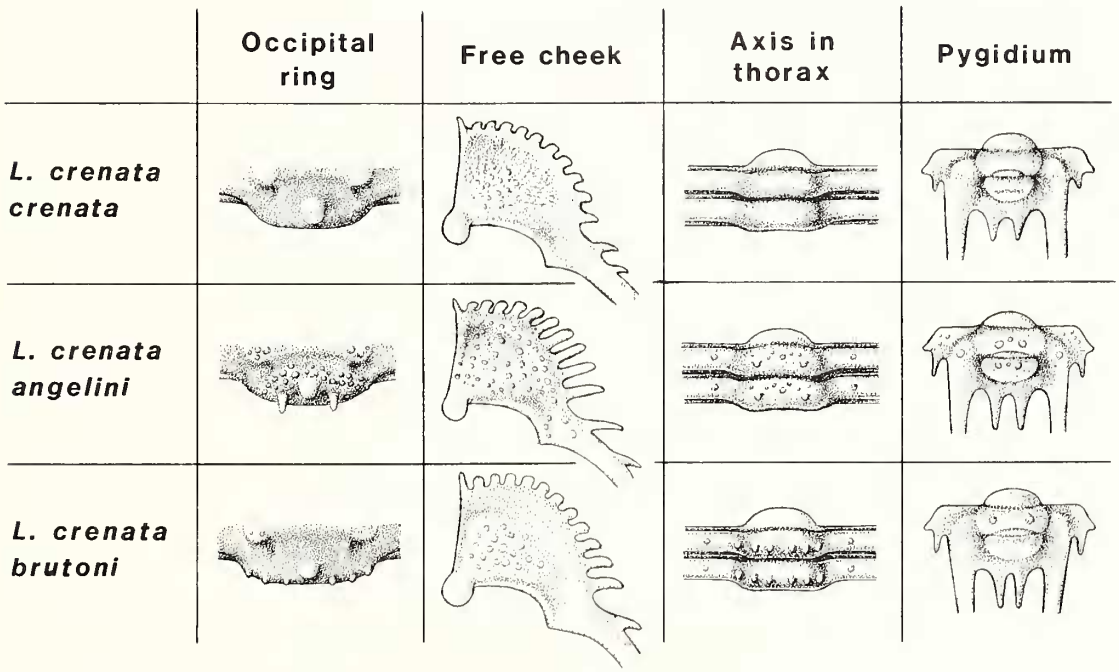
* 1844 *Odontopleura crenata* Emmrich, p. 17.
v. 1967 *Leonaspis crenata* (Emmrich, 1844); Bruton, p. 224, pl. 32, figs. 3–8, pl. 33, figs. 1, 2, 5, pl. 34, figs. 1, 2 [with synonymy list].
. *1969* *Leonaspis crenata* (Emmrich, 1844); Schrank, p. 710.
. *1977* *L. crenata* (Emmrich); Campbell, p. 113.
. *1978* *L. crenata* (Emmrich); Šnajdr, p. 35.
. *1981* *L. crenata crenata* (Emmrich, 1844); Thomas, p. 92.

Lectotype. Selected Bruton, 1967, p. 224; specimen in the Geological-Paleontological Museum, Humboldt University, East Berlin, HU MB 1963/29/1, incomplete cephalon with part of thorax, one of two syntypes from the Emmrich Collection, figured Bruton 1967, pl. 32, fig. 3, from Djupvik, Eksta parish, Mulde Beds, lower part.

Other material. Over a hundred more-or-less complete, enrolled specimens, plus some disarticulated material, are known from the harbour at Djupvik. The only other known locality is Mulde Tegelbruk 1, Eksta parish (Mulde Beds, undifferentiated). Washed marls from that locality have yielded several fragments, mainly of cheeks and pygidia.

Diagnosis. Occipital ring smooth except for short, stout, blunt median spine. Anterior border with row of about fourteen to sixteen tubercles. Free cheek with indistinct, shallow border furrow and weakly convex to flat border. Twelve border spines, the ten anterior short, rectangular. Genal spine long, slender, without secondary spines on dorsal surface. Cephalon finely tuberculated. Thoracic axis and anterior pleural ridges smooth. Pygidium with short secondary spines. Second axial ring well defined posteriorly. Pleural ridges with pair of small tubercles, pygidium otherwise smooth, major spines granulated.

Discussion. This taxon was described comprehensively and figured by Bruton (1967). The term 'bifid spine' should not be applied to the anterolateral corner of the pygidium since there is no spine, but merely a process carrying the articulating facet. I have prepared unworn cranidia, and there is no trace of occipital spines besides the median one; this is the main feature distinguishing the subspecies. A comparison between the three subspecies of *L. crenata* is given in text-fig. 4.



TEXT-FIG. 4. Comparison of some morphological features in the three subspecies of *Leonaspis crenata* (Emmrich, 1844). The different elements are not drawn at the same scale. The distal part of the genal spine and major pygidial spines are omitted.

Leonaspis crenata angelini (Prantl and Přibyl, 1949)

Plate 29, figs. 3, 5–7, 11, Plate 30, figs. 1–4, 8–13, text-fig. 4

v. 1851 Angelin, pl. 22, fig. 14 [illustration only, without name].
. 1854 *Acidaspis barrandei* Angelin, p. 38 [referring to 1851 figure].
. 1885 *Odontopleura Barrandei* Angelin; Roemer, p. 219 (376), pl. 10, fig. 9 [*fide* Schrank 1969].
. *1885* *Acidaspis barrandei* Angelin; Lindström, p. 53.
. *1896* *Acidaspis Barrandei* Ang.; Lake, p. 240.
v* 1949 *Acanthaloma angelini* Prantl and Přibyl, p. 159, pl. 10, figs. 11, 12.
v. 1967 *Leonaspis angelini* (Prantl and Přibyl, 1949); Bruton, p. 228, pl. 34, figs. 3–6.
. 1969 *Leonaspis angelini* (Prantl and Přibyl, 1949) (?); Schrank, p. 717, pl. 6, fig. 9, pl. 7, figs. 1–8, pl. 8, figs. 1, 2.
. *1975* *L. angelini* (Prantl et Přibyl); Šnajdr, p. 315.
. *1978* *L. angelini* Prantl and Přibyl; Šnajdr, p. 35.
v. *non 1979* *Leonaspis angelini* (Prantl and Přibyl); Bruton *in* Jaanusson *et al.*, p. 116 [= *L.* sp. A of this paper].
. *1981* *L. angelini* (Prantl and Přibyl); Clarkson and Howells, p. 529.
. *1981* *L. crenata angelini* (Prantl and Přibyl, 1949); Thomas, p. 88.
. *non 1982* *Leonaspis* cf. *L. crenata angelini* (Prantl and Přibyl, 1949); Howells, p. 54, pl. 14, figs. 22, 23 [*non L. crenata angelini* (Prantl and Přibyl, 1949)].

Holotype. By monotypy; Ar30859, almost complete specimen, figured Angelin 1851, pl. 22, fig. 14; refigured Prantl and Přibyl 1949, pl. 10, figs. 11, 12; refigured Bruton 1967, pl. 34, figs. 4–6; refigured here Plate 29, fig. 6*a–c*; from Lilla Karlsö, possible Halla Beds equivalents.

Other material. Apart from the holotype, only a fragmentary free cheek (Ar47407, figured Bruton 1967, pl. 34, fig. 3) has previously been known from Gotland. I have collected abundant new material at Djupviksvägen 1 and Nordervik (635350 163845), both Ekstа parish, Mulde Beds, undifferentiated but higher than the horizon yielding *L. crenata crenata*. *L. crenata angelini* is also known from 'Graptolithengestein' erratics of a slightly younger age (see Schrank 1969).

Diagnosis. Occipital ring with stout, short, blunt, vertical median spine bearing occipital organ, flanked by pair of slender, pointed spines. Anterior border with row of about fourteen to eighteen tubercles. Free cheek with deep border furrow and convex (tr.) border. All twelve border spines round in section, the anterior four or five with swollen tips, the posterior pointed. Cephalon densely tuberculate. Thoracic axial rings with pair of pointed spines, decreasing in size backwards, anteromedian tubercle, and several symmetrically arranged smaller tubercles. Pygidium with long secondary spines. Second axial ring poorly defined posteriorly. Paired tubercles on axial rings, large tubercle on each pleural ridge, and additional tubercles on axis and anterolateral pleural areas.

Discussion. There are slight differences in coarseness and density of tuberculation between specimens from the three localities in the Mulde Beds: Blåhäll 1, Djupviksvägen 1, and Nordervik. The stratigraphically lowest material, from Blåhäll 1 (Pl. 30, fig. 3*a*), is very similar to the holotype. Specimens from Djupviksvägen 1 (Pl. 29, fig. 3*b*) have a more sparse, coarser tuberculation; specimens from Nordervik (Pl. 29, fig. 5*a*) are even coarser and slightly more densely tuberculated. These differences are small but consistent, but are not regarded here as being of taxonomic importance above the population level.

Thomas (1981, p. 92) regarded the differences between *crenata crenata* and *angelini* to be of subspecific rank only, an approach followed here. Practically all differences between these are due to the strong ornamentation of *angelini*, and from an evolutionary point of view, only a very minor genetic change would be required to produce that effect. Present data suggest that *angelini* is very slightly younger than *crenata crenata*, and so is likely to be its descendant. The material described by Schrank (1969) as *L. angelini* (?) is indistinguishable from Gotland specimens. Thomas (1981) erected *L. crenata brutoni* for British Wenlock specimens differing slightly both from *crenata crenata* and *crenata angelini*. Differences between *brutoni* and the Gotland subspecies were listed by Thomas, all

of which are valid except the notion of *angelini* and *brutoni* lacking an anterolateral 'bifid' spine in the pygidium; this structure is similar in all three subspecies. A comparison between these subspecies is made in text-fig. 4.

Howells (1982, p. 54, pl. 14, figs. 22, 23) figured and described Scottish Llandovery material as 'cf.' (in description) or 'aff.' (in plate explanation) *L. crenata angelini*. The figured pygidium is very wide relative to its length, and has a very small second axial ring, and is on the whole more similar to *L. deflexa* (Lake, 1896). The figured thorax differs from *crenata crenata* in the extremely long pleural spines.

Leonaspis coronata bufo subsp. nov.

Plate 30, figs. 6, 14–16; Plate 31, figs. 1–6

. 1969 *Leonaspis marklini* (Angelin, 1854); Schrank, p. 714, pl. 4, figs. 9, 10, pl. 5, figs. 1–6, pl. 6, figs. 1, 2, 4–7.

Name. Latin *bufo*, toad; referring to the wart-like appearance of the surface sculpture.

Holotype. Ar51664, incomplete cephalon with nine thoracic segments, Plate 30, fig. 14*a–d*, from Djupviksvägen 1, Eksta parish, Mulde Beds, undifferentiated.

Paratypes. All from Eksta parish. From the type locality (Ar51363–51365, Ar51665–51684). From Blåhäll 1, Mulde Beds, lower part (Ar51685, free cheek). From Nordervik (635350 163845), Mulde Beds, undifferentiated (Ar51686–51708). In total about twelve cranidia, sixteen free cheeks, three hypostomes, some thoracic segments, and seventeen pygidia.

Diagnosis. Genal spines very long, reaching about seventh thoracic segment. Thoracic segments with slender, pointed posterior pleural spines, longest on sixth segment, short on anterior three segments, but markedly shortened on anteriormost segment only. Pygidium with major pair of spines directed exsagittally or slightly divergent backwards, secondary spines slender, pointed. Cranidium, base of genal spine, axis, and pygidium coarsely tuberculate.

Discussion. British *coronata* material (see Thomas 1981) and Gotland specimens are of approximately the same age, and are regarded here as geographical subspecies of *L. coronata*. The material from German 'Graptolithengestein' erratics described by Schrank (1969) as *L. marklini* is similar in all features to *bufo*, except possibly a greater range of variation.

None of the previously described or figured Gotland specimens referred to *L. marklini* (Angelin, 1854) are included in *L. coronata bufo*. *L. marklini* is regarded here as a *nomen dubium*. The holotype (see Bruton 1967, pl. 30, fig. 7), a worn external mould of an incomplete exoskeleton, is not identifiable since it lacks important morphological features. The shape and length of the genal spines, the lateral border and border furrow, and the main part of the cranidium, are unknown. No topotype material is known, and the type locality is inaccessible for recollecting. The free cheeks referred by Bruton (1967, pl. 30, fig. 8, pl. 31, figs. 1, 2) to *marklini* are assigned here questionably to *L. muldensis* (see below). Of the other *marklini* material described by Bruton (1967), the pygidia (ibid., pl. 30, figs. 3, 5) may belong to *L. coronata bufo*, or perhaps to *L. muldensis*, the pygidium of which is poorly known, but seems to be similar to that of *bufo*. The cranidia from Lilla and Stora Karlsö (Bruton 1967, pl. 30, fig. 4, pl. 31, fig. 3) have a very narrow median glabellar lobe, especially between the basal lobes, and seem not to belong either to *bufo* or *muldensis*; they cannot be compared with the holotype of *marklini*, which lacks most of the cranidium. The fairly complete specimen figured by Lindström (1885, pl. 13, fig. 15, refigured Bruton 1967, pl. 30, fig. 6) lacks free cheeks and has a median glabellar lobe similar to *bufo* and *muldensis*, but has coarsely tuberculate spines on the thorax and pygidium, and cannot be referred with certainty to either taxon, at least until *muldensis* is better known. The material discussed above cannot be determined specifically; with regard to *Leonaspis* species, the availability of either well-preserved articulated specimens or a complete 'set' of exoskeletal parts from a single locality is a necessity for specific determination.

Two aberrant specimens of *L. coronata bufo* are known. One pygidium (Pl. 31, fig. 5) has an extra, median border spine, probably a genetically determined feature. The pygidium is slightly asymmetrical. One cranidium (Pl. 31, fig. 1) shows a pathological left L2, with the entire cranidium in front of L1 bent sideways. The defect is probably a result of damage during the preceding moult stage.

Leonaspis muldensis Bruton, 1967

v* 1967 *Leonaspis muldensis* Bruton, p. 227, pl. 33, figs. 3, 4, 6, 7.
v? 1967 *Leonaspis marklini* (Angelin, 1854); Bruton, p. 219, pl. 30, fig. 8, pl. 31, figs. 1, 2 [free cheeks only].
. *1978* *L. muldensis* Bruton; Šnajdr, p. 35.

Holotype. Ar30826, enrolled specimen lacking pygidium, figured Bruton 1967, pl. 33, figs. 3, 4, from the harbour at Djupvik (635602 164128), Eksta parish, Mulde Beds, lower part.

Other material, diagnosis, and description. See Bruton 1967, p. 227.

Discussion. Only the three specimens already described by Bruton are known. They are all severely water-worn, lack genal spines and surface sculpture, and only one has the pygidium attached, which is badly worn. From the locality yielding these specimens are also several isolated free cheeks. These were assigned by Bruton (1967) to *L. marklini*, but it seems more likely that they are conspecific with the enrolled specimens from the same beds. This view is neither contradicted nor supported by the morphology of the specimens, since the free cheeks of the enrolled specimens are poorly preserved. On the assumption that *L. muldensis* should be retained as a valid taxon it can easily be distinguished from other *Leonaspis* by the shape of the free cheeks, if these belong to *muldensis*, but is otherwise very similar to *L. coronata* and *L. mutica* (Emmrich, 1844).

L. muldensis occurs together with, and is strongly outnumbered by, *L. crenata crenata*. Similarly, *L. coronata bufo* is always accompanied by, and outnumbered by, *L. crenata angelini*. This occurrence of two *Leonaspis* forms together is common, and has been discussed by several authors (see Campbell 1977, p. 113), and the forms are sometimes referred to as morphs of the same species. In the Gotland examples the forms are assigned to separate species, since the differences are so profound.

EXPLANATION OF PLATE 30

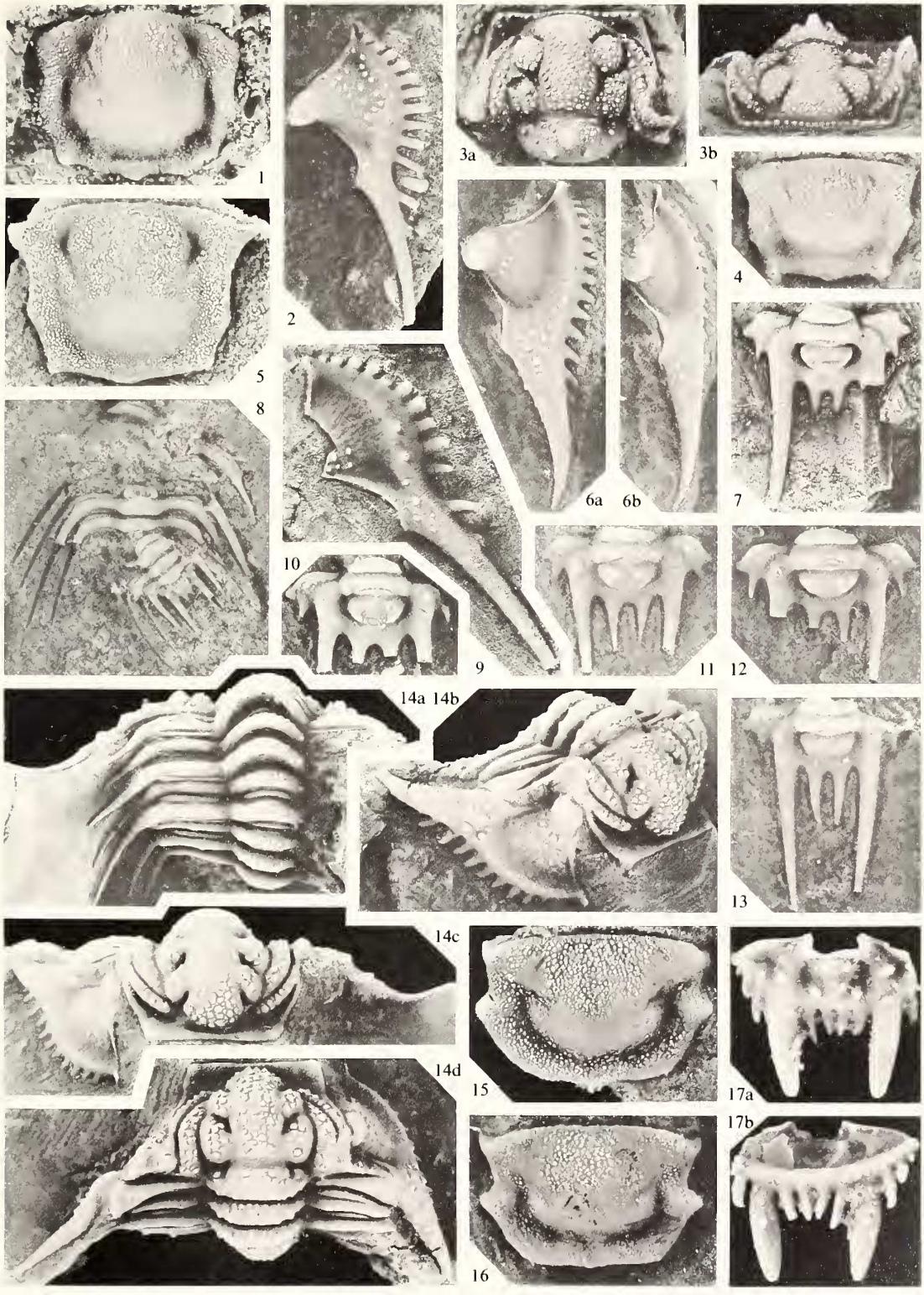
Figs. 1–4, 8–13. *Leonaspis crenata* (Emmrich, 1844) *angelini* (Prantl and Přibyl, 1949). Mulde Beds, lower part (3), Mulde Beds, undifferentiated (1, 2, 4, 8–13). Blåhäll 1 (3), Djupviksvägen 1 (9), Nordervik (2, 4, 8, 10–13), shore south of Djupvik (1). 1, displaced hypostome of complete specimen belonging to K. and W. Amelang, Aachen, exterior view, × 10. 2, Ar51655, free cheek, dorsolateral view, × 5. 3*a*, *b*, Ar51369a, cranidium with dense tuberculation, exterior and anterior views, × 5. 4, Ar51656, small hypostome, exterior view, × 20. 8, Ar51657, disarticulated thorax and pygidium of small holaspis, × 8. 9, Ar51367, free cheek with sparse tuberculation, dorsolateral view, × 6. 10, Ar51658, pygidium, × 6. 11, Ar51659, pygidium, × 6·5. 12, Ar51660, pygidium, × 5. 13, Ar51661, pygidium, × 8.

Figs. 5, 7. *Leonaspis crenata crenata* (Emmrich, 1844). Mulde Beds, lower part, Djupvik. 5, Ar30840, hypostome, exterior view, × 12. 7, Ar30812, pygidium, × 7.

Figs. 6, 14–16. *Leonaspis coronata* (Salter, 1853) *bufo* subsp. nov. Mulde Beds, undifferentiated. Djupviksvägen 1 (14–16), Nordervik (6). 6*a*, *b*, Ar51686,* free cheek, dorsolateral and dorsal views, × 5. 14*a*–*d*, holotype Ar51664, partly disarticulated specimen lacking pygidium, thorax, oblique anterolateral, anterior, and exterior views, × 5. 15, Ar51665,* hypostome, exterior view, × 9. 16, Ar51363,* hypostome, exterior view, × 10.

Fig. 17. *Dudleyaspis* (*Dudleyaspis*) *uncifera* sp. nov. Ar51710,* earliest? holaspid pygidium, dorsal and ventral views, Rönnklint, Upper Visby Beds, × 22.

* Paratypes.



RAMSKÖLD, *Leonaspis*, *Dudleyaspis*

Leonaspis sp. A

Plate 31, figs. 7–11, 13

v. *1979* *Leonaspis angelini* (Prantl and Přibyl); Bruton *in* Jaanusson *et al.*, p. 116, *non* Prantl and Přibyl, 1949.

Material. All specimens are from Visby parish. Högklint Beds, unit b: Vattenfallsprofilen 1, 20·1–20·2 m a.s.l. (SGU 1454–1456). Dump at Visby harbour (639275 164800) (Ar51347). Högklint Beds, undifferentiated: 'Visby' (Ar30878, Ar30879).

Discussion. These specimens may well represent a new species, but more and better-preserved material is needed before it can be established formally. The main distinguishing features are as follows: occipital ring with a stout median spine flanked by a pair of slender spines; median glabellar lobe narrow (tr.), parallel-sided; L1 confluent with cheek laterally due to effaced axial furrow; anterior border with a row of tubercles; anterior margin convex forwards; paired tubercles on glabella; close to facial suture is a spine dorsally on genal spine, but not on posterior margin of cranidium; free cheek with thirteen border spines; genal spine very long, slender; pygidium fairly similar to that of *L. crenata angelini*, but with narrower axis, very large tubercle-pair on pleural ridges, and with a tubercle-pair above bases of posterior border spines.

L. sp. A is closest to *L. crenata angelini*, although the differences are quite marked, especially in the shape of the glabellar lobes. Bohemian Ludlow specimens assigned by Přibyl and Vaněk (1966, p. 295, pl. 2, fig. 1, pl. 3, figs. 3, 4) to *L. geinitziana* (Hawle and Corda, 1847; regarded as a synonym of *L. leonhardi* (Barrande, 1846) by Bruton 1968, p. 20), show some similarity to *L.* sp. A, both in the shape of the glabellar lobes and in the pygidium (if the associated parts of each species really belong together). It differs, however, e.g. in the shape of the occipital ring and the axial furrow, and perhaps in the number of pygidial spines. No close comparison can be made until both species are better known.

EXPLANATION OF PLATE 31

Figs. 1–6. *Leonaspis coronata* (Salter, 1853) *bufo* subsp. nov. Mulde Beds, undifferentiated. Djupviksvägen 1 (1, 2, 4, 5), Nordervik (3, 6). 1, Ar51368a,* cranidium showing pathological asymmetry, ×7. 2, Ar51365,* pygidium, ×6. 3, Ar51688,* latex cast of external mould of pygidium with part of thorax, ×4. 4*a*, *b*, Ar51364,* cranidium, exterior and lateral views, ×4. 5, Ar51684,* pygidium with extra (median) spine, note slight asymmetry, ×7. 6, Ar51687,* pygidium, ×6.

Figs. 7–11, 13. *Leonaspis* sp. A. Högklint Beds, unit b (7, 9–11), undifferentiated (8, 13). Dump at Visby harbour (10), Vattenfallsprofilen 1, 20·1–20·2 m a.s.l. (7, 9, 11, coll. G. Liljevall 1908), Visby (8, 13). 7, SGU 1454, worn pygidium, ×7. 8, Ar30878, small cranidium, exterior view, ×7. 9, SGU 1455, free cheek, dorsolateral view, ×7. 10, Ar51347, partial free cheek, dorsolateral view, ×6. 11, SGU 1456, pygidium, ×7. 13*a*, *b*, Ar30879, cranidium, exterior and anterolateral views, ×6.

Figs. 12, 15–18. *Ceratocephala barrandii* (Fletcher *in* Salter, 1853). Högklint Beds, middle-upper part (15, 17), Halla Beds, unit b (16, 18), undifferentiated (12). Hörsne kanal (16, 18), Ireviken (17), Lilla Karlsö (12), south of Visby cement factory (15). 12, Ar30792, internal mould of partial cranidium, exterior view, ×4 (coll. A. Florin 1891). 15*a*, *b*, SGU 1457, partial thorax and pygidium, exterior view and dorsal view of pygidium, *a* ×2·5, *b* ×3 (coll. G. Liljevall). 16, SGU 1458, anteriormost? thoracic segment, ×2 (coll. G. Liljevall 1909). 17, mainly internal mould of partial cranidium, belonging to K. and W. Amelang, Aachen, exterior view, ×2. 18*a*, *b*, SGU 1459, partly exfoliated cephalon, exterior and anterolateral views, ×2 (coll. G. Liljevall 1909).

Fig. 14. *Ceratocephala* sp. Ar51626, small pygidium, dorsal and ventral views, Rönnklint +7·5 m, Lower Visby Beds, ×13 (coll. V. Jaanusson 1981).

* Paratypes.

RAMSKÖLD, *Leonaspis*, *Ceratocephala*

A few pygidia of *coronata* type are also stated (on the labels) to be from the Högklint Beds, and a second species may thus be present. However, these specimens come from old collections with locality stated only as 'Visby', and a large number of Mulde Beds specimens mislabelled 'Visby' are known, so that the locality quoted must be regarded with caution.

Leonaspis sp.

Material. Ar51758–51765, small fragments of cranidia, free cheeks, thoracic segments and pygidia, from the Lower Visby Beds at Rönnklint (641181 165698), Lummelunda parish.

Discussion. The material is very fragmentary, but may represent a new species. The free cheeks have a very weak lateral border and border furrow, similar to *L. crenata crenata*, but have a secondary spine dorsally on the genal spine, similar to *L.* sp. A described above. An incomplete pygidium has two secondary spines between the major spines. The species is fairly common in the Lower Visby Beds at Rönnklint, and new material will hopefully make a specific assignment possible.

Subfamily MIRASPIDINAE Richter and Richter, 1917
Genus CERATOCEPHALA Warder, 1838

Type species. By monotypy; *Ceratocephala goniata* Warder, 1838, from the middle Silurian, Springfield, Ohio.

Ceratocephala barrandii (Fletcher *in* Salter, 1853)

Plate 31, figs. 12, 15–18

v. 1851 Angelin, pl. 21, fig. 7 [illustration only, without name].
* 1853 *Acidaspis Barrandii* Fletcher *in* Salter, pl. 6, p. 6.
v. 1854 *Trapelocera bicuspis* Angelin, p. 31 [referring to 1851 figure].
v. *1933* *Ceratocephala bicuspis* (Angelin); Warburg, p. 13.
v. 1967 *Ceratocephala bicuspis* (Angelin, 1854); Bruton, p. 241, pl. 36, fig. 11 [with synonymy list].
1981 *Ceratocephala barrandii* (Fletcher *in* Salter, 1853); Thomas, p. 94, pl. 24, figs. 11–14, 18–23, pl. 25, figs. 1–7 [with synonymy list].

Material. From Visby, most probably Högklint Beds, units b and c; Ar2184, partial cephalon, holotype of *T. bicuspis* Angelin; Ar6152, partial thoracic segment; SGU 1457, partial thorax and pygidium. From Hörsne kanal (638493 166725), Hörsne parish, Halla Beds, unit b; SGU 1458–1459, cephalon and partial thoracic segment (the two specimens discussed by Warburg 1933, p. 13). From Lilla Karlsö, ?Halla Beds; Ar30792, partial cranidium.

Discussion. This species was described recently by Thomas (1981). The Gotland material is identical to British specimens and *T. bicuspis* Angelin, 1854 is accordingly considered to be a junior subjective synonym of *A. barrandii* Fletcher *in* Salter, 1853. The few Gotland specimens do not add any new information on the morphology of the species.

Ceratocephala sp.

Plate 31, fig. 14

Material. Ar51626 (small pygidium), Ar51751–51756 (fragments of thoracic segments and pygidia), all from the Lower Visby Beds at Rönnklint (641181 165698), Lummelunda parish.

Discussion. One incomplete large and one small pygidium (Pl. 31, fig. 14) both have only three marginal spines. This is a feature unique among Silurian *Ceratocephala*, and the material almost certainly represents a new species. It may be related to *C. barrandii* since one fragment is probably a free distal part of the tenth thoracic segment, indicating the presence of a structure similar to that described by Thomas (1981, p. 94) for *barrandii*. Several Ordovician species also have three-spined pygidia and sutures on the tenth thoracic segment, but the Gotland specimens seem distinct from each of these, although a comparison is not meaningful without more material.

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